



# Challenging the distribution shift: Statically-induced direction illusion implicates differential processing of object-relative and non-object-relative motion

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## ABSTRACT

The direction illusion is the phenomenal exaggeration of the angle between the drift directions, typically, of two superimposed sets of random dots. The direction illusion is commonly attributed to mutual inhibition between direction-selective cell populations (distribution-shift model). A second explanation attributes the direction illusion to the differential processing of relative and non-relative motion components (differential processing model). Our first experiment demonstrates that, as predicted by the differential processing model, a static line can invoke a misperception of direction in a single set of dots – a phenomenon we refer to as the statically-induced direction illusion. In a second experiment, we find that the orientation of a static line can also influence the size of the conventional direction illusion. A third experiment eliminates the possibility that these results can be explained by the presence of motion streaks. While the results of these experiments are in agreement with the predictions made by the differential processing model, they pose serious problems for the distribution-shift account of shifts in perceived direction.

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## 1. Introduction

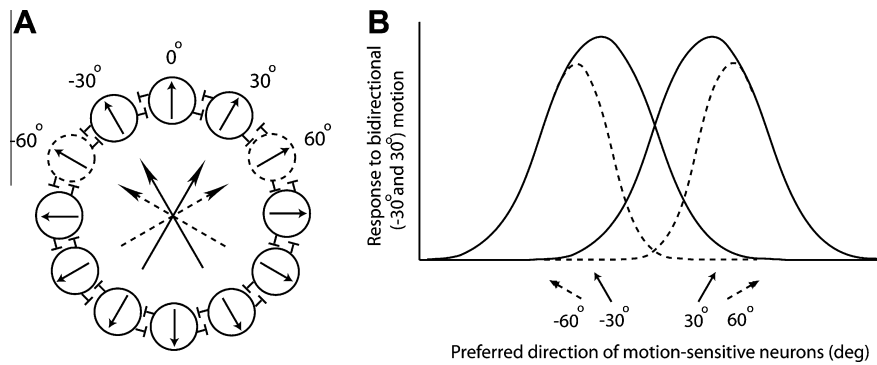
Our perception of the motion of an object is determined both by its spatial context and the motion of the object itself. An everyday example of the influence an object's spatial context has on its perceived motion comes from Rubin (1927), who described an observer's perception of a passenger waving with vertical hand movements from the window of a passing train. The observer does not perceive the passenger's hand tracing out a sine wave, which is its path of motion relative to the observer (veridical motion). Instead, the train becomes a perceptual frame of reference, and the hand is seen as oscillating vertically, relative to the train. Effects of spatial context on perceived motion have long been used in studies of the human visual system (e.g. Duncker, 1929/1955). One such effect, known as the direction illusion, is the phenomenal exaggeration of the angle between the respective directions of two stimuli translating in the frontoparallel plane (Marshak & Sekuler, 1979; Mather & Moulden, 1980). The direction illusion is typically observed in transparent motion displays, such as bidirectional random dot kinematograms (RDKs), which consist of two superimposed sets of random dots moving continuously, each in a different direction.

### 1.1. Distribution-shift model

The direction illusion is generally thought to arise from mutual inhibition between direction-selective cell populations that are most responsive to the two veridical directions in the display, as postulated by the distribution-shift model (e.g. Mather, 1980; Mather & Moulden, 1980) (Fig. 1A). The distribution-shift model is based on the premise that a stimulus moving in a constant direction in the frontoparallel plane evokes responses in a population of cells tuned to a continuum of directions of motion. The activity in these cells can be represented by an approximately Gaussian distribution, with its peak indicating the responses of cells tuned specifically to the stimulus' veridical direction, and its tapering flanks corresponding to the responses of cells tuned to increasingly divergent directions (e.g. Albright, 1984) (Fig. 1B). Cells that usually respond maximally to a given direction are inhibited when a second stimulus of a different direction is presented simultaneously (see Snowden et al., 1991). However, cells tuned to more divergent directions are less inhibited by the additional stimulus. The distributions thus become skewed, so that cells less affected by the inhibition are now the cells most responsive to the stimulus. As a result, the peaks of the two response distributions shift apart, invoking a percept of the two directions being more divergent than they actually are. Mutual inhibition thus distorts the perceived motion trajectories in a way that has been described as direction 'repulsion' (Marshak & Sekuler, 1979; Rauber & Treue, 1999; Raymond, 1993). The distribution-shift model is widely considered

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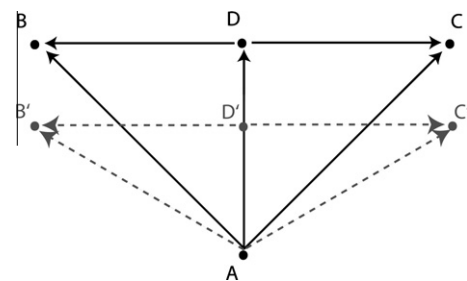
**Fig. 1.** Diagrams depicting the distribution-shift model (Mather & Moulden, 1980). (A) An explanation of direction repulsion as resulting from mutual inhibition between direction-selective cell populations (adapted from Hiris and Blake (1996)). When presented with a bidirectional (e.g.  $\pm 30^\circ$ ) stimulus (solid central arrows), cells tuned to vertical are most inhibited, since these cells are equally responsive to either direction. The cells tuned maximally to the two stimulus directions are also inhibited to an extent so that the cells tuned to more divergent directions (dashed circular outlines) are now the most responsive, resulting in a perceptual exaggeration of the difference between the two directions (dashed central arrows). (B) The hypothetical responses (not to scale) of a population of direction-selective cells to a particular stimulus can be represented by a Gaussian distribution. When two directions ( $\pm 30^\circ$ ) are presented simultaneously, activation of cells that respond to both directions is suppressed. The distributions thus become skewed, such that cells tuned to, say,  $-60^\circ$  are now most responsive to the  $-30^\circ$  stimulus. Thus, the population response to a  $-30^\circ$  stimulus now evokes a percept of a stimulus moving at  $-60^\circ$ .

as applying to the domain of motion direction. However, an essentially identical model was originally introduced to account for distortions in perceived orientation, namely the tilt illusion – the phenomenal exaggeration of the angle between two differently oriented static lines (Blakemore, Carpenter, & Georgeson, 1970). Like the direction illusion, the tilt illusion has been attributed to mutual inhibition, but between orientation- rather than direction-selective cell populations (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Wenderoth, O'Connor, & Johnson, 1986).

### 1.2. Differential processing model

Dakin and Mareschal (2000) argued that mutual inhibition between direction-selective channels does not explain certain aspects of the direction illusion, and they presented a variation of the phenomenon to demonstrate this. Two sets of dots with a direction separation of  $45^\circ$  would normally yield a large direction illusion (e.g. Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007). Dakin and Mareschal found that including a third set of dots drifting at sufficient speed in a direction opposite to the vector average direction of the first two eliminated the effect. They asserted that the distribution-shift model makes no such prediction. However, there is a possible problem with discounting the distribution-shift model based on this finding alone. Although the third set was directionally distant from the other two sets ( $\pm 157.5^\circ$ , respectively), and although repulsion in many cases is found to persist only up to direction separations of  $120\text{--}135^\circ$  (e.g. Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007), Dakin and Mareschal (2000) themselves, in another experiment from the same paper, recorded significant repulsion with a direction separation of  $135^\circ$ . Moreover, we know that the greater the ratio of speeds for the two sets of dots (up to a ratio of  $\sim 2:1$ ), the greater the shift in the slower set (Benton & Curran, 2003; Dakin & Mareschal, 2000; Kim & Wilson, 1996; Lindsey, 2001; Marshak & Sekuler, 1979). Hence, the possibility remains that, through mutual inhibition, the third set of dots was invoking counteractive angular repulsion on each of the other sets to cancel out the initial direction illusion. Notwithstanding this possibility, Dakin and Mareschal (2000) suggested that the phenomenon could be more adequately explained in terms of an alternative model. They proposed that the direction illusion results instead from the differential processing of two types of relative motion, similar to that described by Johansson (1950). Johansson (1950) contended

that the veridical velocity of an object is perceptually broken down into two component velocities: an object-relative component and a non-object-relative component. He described the object-relative component as the motion that is 'unique' to the object and the non-object-relative component as that which is 'common' to all objects in the visual field with respect only to the observer. Returning to Rubin's example, the veridical sinusoidal motion of the waving hand is parsed into object-relative and non-object-relative components, being respectively its vertical motion relative to the train and the horizontal motion common to both the train and the hand. Johansson further asserted that the non-object-relative component velocity provides a reference frame for the object-relative component velocity of each object. Accordingly, the hand in Rubin's example is perceived as oscillating vertically. Johansson demonstrated that this object-relative component is the 'dominant' percept, so that, for example, when two objects seen against a homogeneous background move at equal speed in orthogonal directions from a common point, they are perceived as moving directly away from each other. Orthogonal to this, the non-object-relative component is also detected but is perceptually 'secondary in character' and not always apparent (Johansson, 1950). According to Dakin and Mareschal (2000), differential processing can potentially account for the direction illusion in much the same way: if the non-object-relative component velocity is perceptually underestimated with respect to that of the object-relative component, the directional separation of the two sets of dots in a bidirectional RDK will be perceptually exaggerated (Fig. 2).



**Fig. 2.** Vector diagram of the differential processing account of the direction illusion. Vectors AB and AC represent the veridical trajectories of two sets of dots. The non-object-relative component AD is, with respect to the object-relative component velocities D'B' and D'C', perceptually underestimated, as AD'. This results in a perceptual exaggeration of  $\angle BAC$  as  $\angle B'AC'$  (adapted from Dakin and Mareschal (2000)).

### 1.3. Supporting evidence for differential processing

Johansson's work is descriptive rather than explanatory. However, empirical justification for postulating the differential processing model comes from numerous psychophysical studies showing that separate neural processes facilitate the extraction of object-relative and non-object-relative component velocities, and that our visual system is more responsive to object-relative than to non-object-relative motion. Velocity and displacement detection thresholds (Beardsley & Vaina, 2008; Lappin, Donnelly, & Kojima, 2001; Legge & Campbell, 1981; Leibowitz, 1955; Mack, Fisher, & Fendrich, 1975; Shioiri et al., 2002; Snowden, 1992; Sokolov & Pavlova, 2006) and reaction times (Smeets & Brenner, 1994), for example, are lower for object-relative than for non-object-relative motion perception. Changes in stimulus luminance contrast have been found to differentially affect detection of object-relative and non-object-relative velocities. Grossman and Blake (1999) used an RDK to investigate the effects of low and high luminance conditions on object-relative and non-object-relative motion. Detection of object-relative motion required detection of a region within the RDK defined by the offset trajectories of a number of dots as they moved over the area. They found that while low luminance levels impaired the detection of object-relative motion, they did not diminish detection of non-object-relative motion. In another study, Levinson, Coyne, and Gross (1980) found that when contrast was reduced to peri-threshold levels, a bi-directional RDK with an angular separation of 30° was seen as a single sheet of dots moving in a direction midway between the two component directions. The reported percept therefore corresponded with observers perceiving the non-object-relative component motion only, showing again that object-relative and non-object-relative motion perception are differentially affected by changes in contrast. Moreover, the speed of a stimulus in non-object-relative motion has been found to be perceptually underestimated in comparison to one viewed in object-relative motion (Blakemore & Snowden, 2000; Brown, 1931; De Bruyn & Orban, 1999; Gogel & McNulty, 1983; Nguyen-Tri & Faubert, 2007; Norman et al., 1996). Brown (1931) compared the perceived velocity of dots moving against a homogeneous background with dots moving against a textured background and found the latter to appear 25% faster. Gogel and McNulty (1983) found increases of up to 42% in the perceived speed of a translating spot of light as the density of reference cues was increased from 0.1 to 0.65 marks/cm. Similar results have been reported in a subsequent study (Ornan, 2009). Norman et al. (1996) found that the perceived speed of a central region of random dots was higher in the presence of a surrounding region of stationary dots than when the stationary dots were absent. Blakemore and Snowden (2000) found that a dot moving across a high-contrast background appears faster than a dot moving across a low-contrast background. De Bruyn and Orban (1999) compared the perceived speed of a set of dots when presented alone and when in transparent motion with a second set of dots moving in the opposite direction. The perceived speed was found to be 50% greater in the transparent motion condition. All of these studies indicate that objects viewed in object-relative motion are perceived as being faster than objects of equal veridical speed viewed in non-object-relative motion. Taken together, the results from the above studies constitute ample justification for considering the differential processing of object-relative and non-object-relative component velocities as a possible mechanism underlying the contextual determination of perceived stimulus direction, as in the case of the direction illusion.

### 1.4. Current objectives

The aim of the current paper was to evaluate and compare the adequacy of both the distribution-shift and differential processing

models in accounting for the perception of stimulus direction. To this end, taking a similar approach to Dakin and Mareschal (2000), we presented new variations of the conventional direction illusion-invoking stimulus configuration that allowed distinct predictions to be made by each model. Specifically, we investigated the effects of a static line stimulus on the perceived direction of a unidirectional set of dots (Experiment 1), as well as on the perceived direction of one of the sets of dots in a bidirectional direction illusion-invoking display (Experiment 2). We also investigated whether a more broadly defined distribution-shift model might account for the results (Experiment 3).

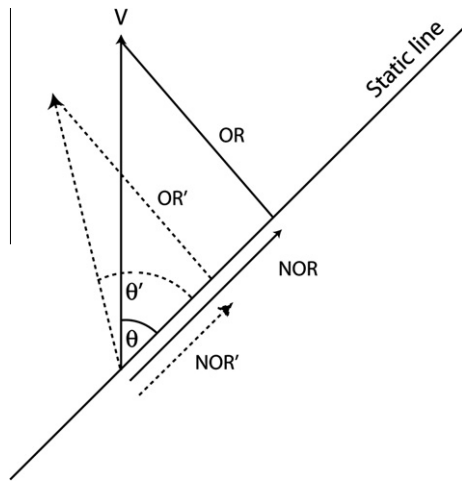
## 2. Experiment 1

When the endpoints of a moving line are obscured, such as when it is viewed through a circular aperture, the line will appear to move in a direction orthogonal to its orientation, since the endpoints provide the only cue to any motion of the line parallel to its orientation. This is the well-known 'aperture problem' (Wallach, 1935). The same effect can be achieved without the aperture if the endpoints can be otherwise obscured, such as if the line extends beyond a certain eccentricity, particularly if the line's contrast is tapered towards its endpoints, since the visual system has a lower acuity and higher contrast detection threshold for stimuli in the periphery (see Anstis, 2003). Similarly, such a line, if presented as a stationary reference for other moving elements, will provide no positional reference cues along the axis of its orientation. Since object-relative motion by definition requires reference points and non-object-relative motion by definition requires the absence of reference points, any motion orthogonal to that axis will be object-relative and (in the complete absence of all other visual references) any motion parallel to that axis will be non-object-relative motion. The differential processing model dictates that any unidirectional motion oblique to the line will be parsed by the visual system into a non-object-relative component parallel to the line and an object-relative component orthogonal to the line. Further, because of the visual system's greater responsivity to object-relative than to non-object-relative motion, the velocity component parallel to the line (non-object-relative) will be perceptually reduced in comparison to that orthogonal to the line (object-relative). The direction of a stimulus such as a set of dots drifting obliquely to the line should therefore be shifted perceptually towards the orthogonal, i.e. the direction of the dots should be 'repelled' by the orientation of the line (Fig. 3). This predicted shift in perceived direction of a single set of dots invoked by the presence of the static line we will refer to as the statically-induced direction illusion. The distribution-shift model, on the other hand, makes no such prediction since, by definition, it requires the presence of two directions of motion. The current experiment was designed to test for the occurrence of a statically-induced direction illusion and, if one was observed, to ascertain how the angular difference between the orientation of the inducing line and the test direction affects the magnitude of the illusion. This would enable us both to draw comparisons with previously obtained angular functions of the conventional direction illusion and to determine the optimal stimulus parameters for use in later experiments.

### 2.1. Method

#### 2.1.1. Apparatus

All stimuli were generated and presented and all responses recorded with Psykinematix version 1.1.0 (build 1011) (KyberVision, Montreal, Canada, [psykinematix.com](http://psykinematix.com)). The software was run on a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame



**Fig. 3.** The dissociation of object-relative (OR) and non-object-relative (NOR) component velocities of a drifting stimulus due to the presence of a stationary line. The veridical velocity ( $V$ ) is vertically upward, while its object-relative and non-object-relative component velocities are respectively orthogonal and parallel to the static line. We hypothesise that the non-object-relative component velocity will be perceptually underestimated (as  $NOR'$ ) with respect to the object-relative component, resulting in the angular separation of the drifting stimulus direction and the orientation of the line ( $\theta$ ) being perceptually exaggerated ( $\theta'$ ).

refresh rate of 75 Hz and a pixel resolution of  $1152 \times 870$ . Participants viewed the screen binocularly from a distance of 57 cm through a cylinder (diameter 30 cm, length 57 cm) that was lined internally with matte black felt, and a chin and headrest prevented head movement.

### 2.1.2. Stimuli

A unidirectional white-on-grey RDK (test stimulus) comprising a coherently drifting set of 40 Gaussian dots was presented within an 8-deg virtual aperture with no visible boundary. All dots had a peak luminance of  $104 \text{ cd/m}^2$ , with a standard deviation of 6 min-arc and a drift speed of  $0.5 \text{ deg/s}$ . The background luminance was  $65 \text{ cd/m}^2$ , giving a Michelson contrast of 23.1%. Dependent upon each observer's responses, the test stimulus drifted in a range of directions close to upward vertical ( $0^\circ$ ). The inducing stimulus was a static white line (length 27.78 deg, and width 0.12 deg) whose midpoint was located in the centre of the display. The luminance profile along the line's length followed a sin curve ( $0.018 \text{ cpd}$ ) with maximum contrast (23.1%) at the line's midpoint, decreasing to 0% contrast at each endpoint. The line was presented at one of seven orientations ( $3^\circ$ ,  $7.5^\circ$ ,  $15^\circ$ ,  $30^\circ$ ,  $45^\circ$ ,  $60^\circ$ ,  $75^\circ$ , and  $90^\circ$ ) relative to the test direction (positive values indicate clockwise (CW) directions). A baseline condition incorporating an RDK but no inducing line was also presented.

### 2.1.3. Observers

Twenty-two 2nd-year psychology students at Macquarie University completed the experiment. All were inexperienced observers and none were aware of the purpose of the study. All were emmetropic or had corrected-to-normal vision.

### 2.1.4. Procedure

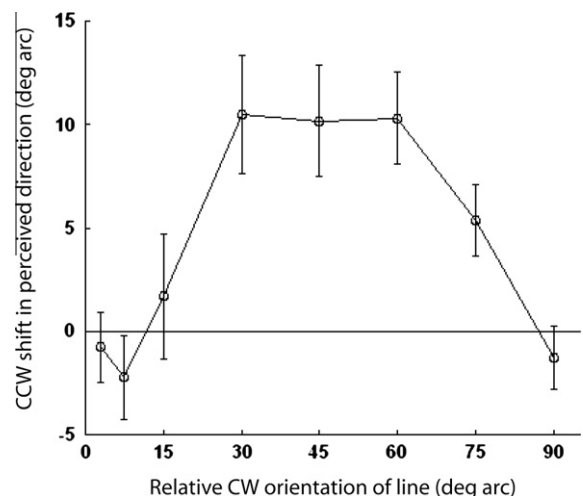
Each trial began with a brief tone and a 500 ms presentation of a uniform grey field with a small point in the centre of the screen. Test stimuli were then presented for 500 ms, during which time the central point was not present. Observers were instructed to remain fixated as near as possible to where the point had initially been presented. Being the centre of the display, this point coincided with the midpoint of the static line. Each successive trial

began once a response was made. The seven test conditions were fully randomised within a single block of trials. The baseline condition was run in a separate block. This study used a standard staircase method (Wetherill & Levitt, 1965) to estimate each observer's point of subjective vertical. Observers indicated, using the left and right arrow keys, which side of upward vertical ( $0^\circ$ ) they perceived the test stimulus to be moving. Observers completed two randomly interleaved 1-up-1-down staircases with respective starting values of  $\pm 10^\circ$  from vertical, for each condition. Initial step size was  $5^\circ$ , reducing to  $4^\circ$ ,  $3^\circ$ ,  $2^\circ$ , and a minimum of  $1^\circ$  on subsequent reversals. Each staircase terminated after 12 reversals, with the direction of the test stimulus on the final 6 reversals from each staircase being averaged for each observer to serve as an estimate of perceived vertical. Obtained means were adjusted by subtracting individual values of perceived vertical measured in the baseline condition.

## 2.2. Results and discussion

The results from Experiment 1 are reported in Fig. 4. Directional shifts were small or absent when test/inducer separations were either very small ( $\leq 15^\circ$ ) or very large ( $90^\circ$ ). However, intermediate separations yielded large CCW shifts in perceived direction. A set of one-sample two-tailed  $t$ -tests showed CCW shifts significantly different from zero for each of the  $30^\circ$ ,  $45^\circ$ ,  $60^\circ$ , and  $75^\circ$  conditions ( $t_{(19)} \geq 6.43$ ,  $p < 0.0005$ ,  $\eta^2 \geq 0.685$ ), and no significant shift for the  $3^\circ$ ,  $7.5^\circ$ ,  $15^\circ$ , or  $90^\circ$  conditions ( $t_{(19)} \leq 2.29$ ,  $p \geq 0.034$ ) ( $p$ -values were Bonferroni-adjusted to control for overall error rate). Two of the observers produced anomalous data that indicated an obvious inability or reluctance to follow the instructions. Their data were therefore omitted from the analysis.

The primary aim of the current experiment was to test for the occurrence of a statically-induced direction illusion, which we found. Since mutual inhibition between direction-selective channels could only occur when two directions of motion are presented together, the illusions observed here cannot be accounted for by the distribution-shift model. On the other hand, the occurrence of the phenomenon is predicted by the differential processing model. The peak illusory effect was only  $\sim 10^\circ$ , while the peak effect obtained in most direction illusion studies is  $\sim 20^\circ$  (Grunewald, 2004; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1998; Wiese & Wenderoth, 2007) (see also our results from Experiment 2). Discrepancies between the angular functions of the statically-induced direction



**Fig. 4.** Graph showing the results of Experiment 1. Error bars represent 95% confidence intervals.



illusion and those previously reported for the conventional direction illusion are not surprising, however, due to the differences between the stimuli used to invoke the respective illusions.

### 3. Experiment 2

Having demonstrated the existence of a statically-induced direction illusion, we wished to determine whether the magnitude of a conventional direction illusion could be increased and/or reduced by including differently orientated visual reference cues in the display. Here, we investigated the effects of the orientation of a static line on the perceived direction of one of the sets of dots in a bidirectional RDK.

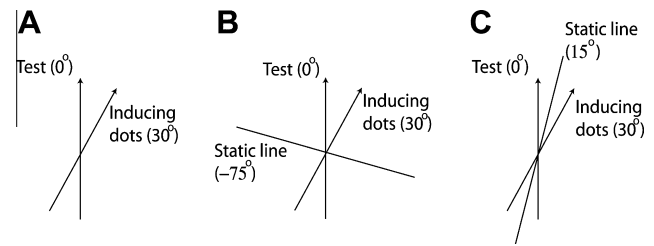
According to the logic of the differential processing account, the introduction of a static line oriented parallel to the object-relative component velocity direction in a bidirectional RDK (parallel to BC in Fig. 2), will provide a reference cue for motion in the non-object-relative component direction (AD in Fig. 2), transforming what was initially non-object-relative motion into object-relative motion. What was initially the object-relative component velocity should be unaffected since the line does not introduce any further reference for motion along its axis. The line should therefore diminish the size of the direction illusion. Conversely, a line parallel to the non-object-relative component velocity should not affect the direction illusion magnitude, since a line with such an orientation would provide no reference along the axis of the non-object-relative component velocity. It would only provide an additional reference along the axis of the object-relative component velocity where references cues are already available. However, there is a possibility that the additional reference will slightly increase the object-relative component velocity, thereby marginally increasing the size of the direction illusion.

The distribution-shift model, however, contends that the mutual inhibition that arises in a bidirectional RDK is driven by the veridical velocities of the two sets of dots invoking responses in direction-selective channels. As these units show no response to stationary features, this model cannot predict that the presence of a static line of any orientation should have an influence on the magnitude of the direction illusion.

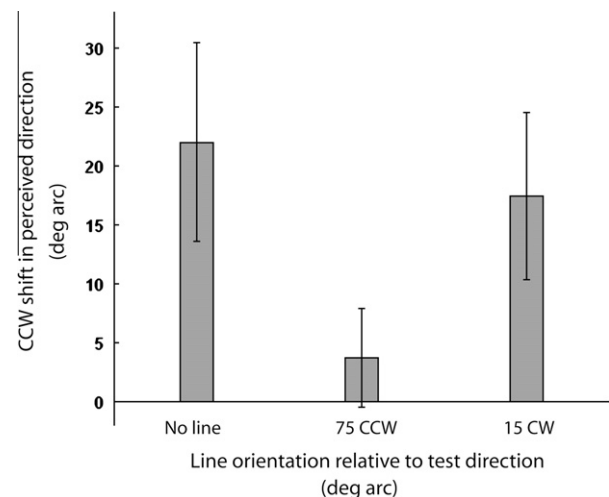
The current experiment was designed to determine whether or not the magnitude of the direction illusion observed in a bidirectional RDK would be reduced by the presence of a static line oriented orthogonally to the non-object-relative component velocity, and either increased or unaffected with the line oriented parallel to the non-object-relative component velocity.

#### 3.1. Method

The apparatus was identical to that in Experiment 1, but several changes were made to the stimulus configuration. Here we used bidirectional RDKs with one set of dots considered the test stimulus and the other the direction illusion inducer, which drifted at  $30^\circ$  relative to the test direction. The  $30^\circ$  direction separation was chosen on the basis that the same separation yielded the largest statically-induced direction illusion in Experiment 1. The experiment included three conditions, one of which consisted of the bidirectional RDK alone (Fig. 5A), and two of which also incorporated the static white line, which was oriented at either  $-75^\circ$  or  $15^\circ$  relative to the test direction (see Fig. 5B and C). The two orientations were specifically selected to match the direction of the object-relative and non-object-relative component velocities, respectively. The three test conditions were fully randomised within a single block of trials. Obtained means were adjusted by subtracting individual values of perceived vertical measured in the baseline condition in Experiment 1.



**Fig. 5.** Schematic diagram of the three test conditions in Experiment 2: (A) Bidirectional RDK with test direction  $0^\circ$  and inducing dots direction  $30^\circ$  relative to test direction. (B) Bidirectional RDK with a static line oriented at  $-75^\circ$  relative to the test direction, i.e. aligned with the object-relative component velocities. (C) Bidirectional RDK with a static line oriented at  $15^\circ$  relative to the test direction, i.e. aligned with the non-object-relative component velocity.



**Fig. 6.** Graph showing the results of Experiment 2. Error bars represent 95% confidence intervals.

#### 3.1.1. Observers

Twenty-one of the 22 observers who participated in Experiment 1 also participated in Experiment 2.

#### 3.2. Results and discussion

Data from five of the observers, including those omitted in Experiment 1, were omitted from the current analysis, the reason being that three observers produced results in the direction illusion condition indicating a CW shift in perceived direction, opposite to the expected shift.<sup>1</sup> Results from Experiment 2 are reported in Fig. 6. For the no-line (direction illusion) condition we obtained a mean CCW directional shift of  $22.0^\circ$ , which is similar in size to previous measurements of the direction illusion with the same directional separation of  $30^\circ$  (Braddick, Wishart, & Curran, 2002; Grunewald, 2004; Rauber & Treue, 1999; Wiese & Wenderoth, 2007). With a line oriented at  $75^\circ$  CCW of the test direction we obtained a mean CCW directional shift of  $3.7^\circ$ , and with a line oriented at  $15^\circ$  CW of the test direction we obtained a mean CCW directional shift of  $17.4^\circ$ . A set of one-sample two-tailed *t*-tests showed the direction illusion in the no-line condition ( $t_{(15)} = 5.511$ ,  $p < 0.0005$ ,

<sup>1</sup> The aim of our study was to compare the capacity of two models to predict characteristics of the direction illusion as it is generally observed. As no previous study has reported an attraction effect when the inducer and test directions are separated by  $30^\circ$ , we considered it prudent to omit these data. However, when these results are included, there is no appreciable change in the pattern of results obtained, or in the statistical significance of the findings.

$\eta^2 = 0.669$ ), and in the 15° CW condition ( $t_{(15)} = 5.203$ ,  $p < 0.0005$ ,  $\eta^2 = 0.643$ ) to be significantly different from zero. However, the small shift in the 75° CCW condition was not significantly different from zero ( $t_{(15)} = 1.861$ ,  $p = 0.082$ ), signifying that the presence of the line in this condition was effective in eliminating the direction illusion. Two-tailed  $t$ -tests showed a significant difference between the no-line and 75° CCW condition ( $t_{(15)} = 6.806$ ,  $p < 0.0005$ ) but no significant difference between the no-line and 15° CW condition ( $t_{(15)} = 1.432$ ,  $p = 0.173$ ).

While the results of the no-line and 15° CW conditions are consistent with a distribution shift, the model cannot account for the results of the 75° CCW condition. On the other hand, the results of all three conditions are readily interpretable if we attribute the direction illusion to differential processing. As predicted by this model, the direction illusion was significantly reduced in the 75° CCW condition, possibly because the non-object-relative component velocity is no longer underestimated when the line is added, since the line effectively transforms this component into an object-relative motion. The direction illusion was unchanged by the presence of the 15° CW line. We can infer from this finding that the object-relative component velocity was unchanged by the additional reference cue.

#### 4. Experiment 3

As described earlier, the distribution-shift model attributes the direction illusion to mutual inhibition between direction-selective cell populations. The previous two experiments have respectively demonstrated the inability of this model to account for the capacity of a static line to invoke a direction illusion (Experiment 1) and to eliminate the direction illusion in a bidirectional RDK (Experiment 2). One way in which we might attempt to reconcile these findings with the distribution-shift model is by considering the possible involvement of mutual inhibition not between direction-selective channels but between orientation-selective channels. We will refer to this proposed mechanism as an orientation distribution shift. Geisler (1999) proposed that moving stimuli produce neural ‘motion streaks’ within the visual system. He suggested that motion streaks should result from the temporal integration of motion signals activating orientation-selective neurons that are tuned to orientations parallel to the direction of motion. If motion stimuli could activate orientation-selective channels, then we should expect to observe perceptual interactions between direction and orientation domains. Geisler provided evidence for the occurrence of motion streaks by measuring the luminance detection threshold of a moving Gaussian dot as a function of its size and speed when it was presented with a grating mask at various orientations relative to the dot direction. When the dot moved above a certain critical speed of approximately 1 ‘dot width’ per 100 ms (a dot width was defined as four times the dot’s Gaussian standard deviation) a parallel mask was significantly more effective in elevating thresholds than was an orthogonal mask, with intermediate mask orientations producing intermediate threshold elevations. Geisler found further evidence for the occurrence of motion streaks in an orientation adaptation experiment. After adaptation to a grating oriented 10° from vertical, observers judged the direction of a vertically moving 12-min dot. The dot had a speed of either 2.5 or 10 deg/s, which according to Geisler’s estimations should produce, respectively, weak and strong motion streaks. While the faster dots showed a shift of  $\sim 2.2^\circ$  in perceived direction, the slower dots were perceptually shifted by only  $\sim 0.4^\circ$ . The former result is comparable in size to the tilt aftereffect, which is a repulsive shift in the orientation of a line or grating due to previous adaptation to a differently oriented line or grating (e.g. Gibson & Radner, 1937). Apthorp and Alais (2009) produced further evidence of motion streaks activating

orientation-selective channels by showing a similar shift in the perceived orientation of a central grating due to simultaneously presented RDK motion surrounding the grating. They obtained an angular function for the effect, which we refer to hereafter as a motion-induced tilt illusion. The results were very similar to those produced in studies of the tilt illusion, which was defined in Section 1.1 (O’Toole & Wenderoth, 1977; Over, Broerse, & Crassini, 1972). Further evidence for direction/orientation interactions comes from studies using static configurations of paired dots that, when flashed in succession, invoke motion percepts whose direction is determined by the orientation of the dot pairs (e.g. Burr & Ross, 2002; Johnson & Wenderoth, 2011; Ross, Badcock, & Hayes, 2000).

The statically-induced direction illusions observed in Experiment 1 are an order of magnitude larger than the direction and orientation shifts associated with the occurrence of motion streaks. Also, in Experiments 1 and 2 we selected values for dot width and speed that would not meet the criteria for producing motion streaks. Remembering that the critical speed is calculated as 1 ‘dot width’ per 100 ms and that a dot width is defined as four times the dot’s Gaussian standard deviation, for a Gaussian dot with a standard deviation of 6 minarc, the ‘dot width’ is 24 minarc. The critical speed was thus 24 minarc per 100 ms, or 4 deg/s. We are therefore confident that the observed effects were not produced, at least not entirely, by this mechanism. However, we wanted to address directly the possible involvement of motion streaks in the production of the statically-induced direction illusion. To this end, we compared the size of the illusion when invoked with RDKs with speeds above and below the critical speed for producing motion streaks. If the illusion is due, at least in part, to mutual inhibition between orientation-selective channels responding to both the static line and motion streaks produced by the drifting dots, i.e. to an orientation distribution shift, we would expect to obtain a larger illusion with the faster dots than with the slower dots. The differential processing model, on the other hand, makes no specific predictions regarding the effects of speed. A further objective was to determine whether the RDK invokes a motion-induced tilt illusion in the static line. If the statically-induced direction illusion arises from an orientation distribution shift due to the presence of motion streaks, we should expect to observe a motion-induced tilt illusion and, as with the statically-induced direction illusion, it should be larger with faster dots than with slower dots. If the statically-induced direction illusion arises entirely from differential processing, however, no motion-induced tilt illusion is expected.

##### 4.1. Methods

###### 4.1.1. Apparatus and stimuli

The apparatus was the same as that used in Experiments 1 and 2. The stimuli differed from those in Experiments 1 and 2 as follows: Here the Gaussian dots had a standard deviation of 3 minarc. Drift speed was either slow (0.5 deg/s) or fast (8 deg/s), respectively below and above the critical speed of 2 deg/s required to produce motion streaks. In the statically-induced direction illusion conditions, the static line was always oriented at 30° relative to the direction of the RDK, and in the motion-induced tilt-illusion conditions, the direction of the RDK was always 30° relative to the orientation of the line.

###### 4.1.2. Observers

Five observers, three male and two female, took part in the experiment. We were confident in using a small group of participants, because the task was relatively simple, and because a pilot study produced robust outcomes. Four of the observers were staff or students at Macquarie University and had previous experience with similar experimental tasks. One participant was the author, and one other was aware of the purpose of the experiment. One

observer had had no previous experience. All were emmetropic or had corrected-to-normal vision.

#### 4.1.3. Procedure

We used four test conditions, labelled SDI slow (statically-induced direction illusion with slow-moving dots), SDI fast (statically-induced direction illusion with fast-moving dots), MTI slow (motion-induced tilt illusion with slow-moving dots), and MTI fast (motion-induced tilt illusion with fast-moving dots). We also ran three baseline conditions: the two statically-induced direction illusion conditions with the static line absent and a motion-induced tilt illusion condition with the RDK absent. In the direction illusion conditions observers judged the direction of the RDK, and in the tilt illusion conditions they judged the line's orientation. The seven conditions were run in separate blocks, which were presented in random order. The procedure was similar to that in Experiments 1 and 2. In each of the experimental conditions, observers completed two randomly interleaved staircases with starting values of  $\pm 20^\circ$  from vertical. Initial step size was  $32^\circ$ , and was halved for each subsequent reversal, with a minimum step size of  $1^\circ$ . Obtained values for each condition were averaged for each observer and adjusted by subtracting individual values obtained from the corresponding baseline conditions.

#### 4.2. Results and discussion

Results from Experiment 3 are reported in Fig. 7. For the SDI slow condition we obtained a mean CCW directional shift of  $13.47^\circ$ , which is comparable in size to that observed in Experiment 1, and in the SDI fast condition we obtained a mean CCW shift of  $2.56^\circ$ . One-sample two-tailed  $t$ -tests showed a significant difference from zero for each of the SDI slow ( $t_{(4)} = 7.763$ ,  $p = 0.001$ ,  $\eta^2 = 0.938$ ), and SDI fast ( $t_{(4)} = 7.034$ ,  $p = 0.002$ ,  $\eta^2 = 0.925$ ) conditions. A paired  $t$ -test showed there was a significant difference in the directional shift between the SDI slow and SDI fast conditions ( $t_{(4)} = 6.463$ ,  $p = 0.003$ ,  $\eta^2 = 0.913$ ). For the MTI slow condition we obtained a mean directional CW shift of  $0.03^\circ$ , and in the MTI fast condition we obtained a mean CW shift of  $0.06^\circ$ . One-sample two-tailed  $t$ -tests showed no significant difference from zero for either the MTI slow ( $t_{(4)} = 0.059$ ,  $p = 0.956$ ) or MTI fast ( $t_{(4)} = 0.098$ ,  $p = 0.926$ ) conditions.

Our failure to observe a motion-induced tilt illusion in either the MTI slow or MTI fast condition indicates either that no motion streaks are produced by our drifting dot stimuli, or that motion streaks are produced but fail to affect the perceived orientation of the line. If the former is the case, then we can immediately

discount the involvement of an orientation distribution shift in producing the statically-induced direction illusion. If the latter is the case, there remains the possibility that the statically-induced direction illusion is produced by an orientation distribution shift but that the shift is asymmetrical, affecting the perceived orientation of the motion streaks, and therefore the perceived direction of the dots, without affecting the perceived orientation of the line. The SDI slow condition yielded a significant shift in perceived direction, indicating that the illusion is not due to the presence of motion streaks, as stimuli at this speed are incapable of forming any such features. Moreover, the shift was an order of magnitude larger than previously reported direction and orientation shifts associated with the interaction of motion streaks and static oriented stimuli (e.g. [Apthorp & Alais, 2009](#)), indicating again that the effects shown in the current study cannot be explained in this way. Conversely, the stimuli in Experiment 3 that were predicted to produce strong motion streaks (SDI fast condition) in fact produced a very much reduced direction illusion. That the SDI slow condition produced a much larger shift than the SDI fast condition clearly contradicts the predictions of the orientation distribution-shift hypothesis and indicates that the statically-induced direction illusion does not arise from the mutual inhibition of orientation-selective cell populations resulting from the occurrence of motion streaks. In contrast, none of the conditions produced data that conflict with the differential processing model. The model makes no predictions of any orientation shift in either of the motion-induced tilt illusion conditions. Further, the SDI slow and SDI fast data are not inconsistent with the differential processing model. Although differential processing explicitly predicts a statically-induced direction illusion in both slow and fast conditions, it makes no specific quantitative prediction regarding the effect of dot speed and, in particular, the relative size of the effects in slow and fast conditions. Further research into the effects of speed on both object-relative and non-object-relative velocities is required before the model can be extended to make any such predictions. However, the current findings echo those previously reported in the context of the direction illusion. Our data show an increase in statically-induced direction illusion magnitude as the RDK speed is reduced from 8 deg/s to 0.5 deg/s. [Raubert and Treue \(1999\)](#) and [Braddick, Wishart, and Curran \(2002\)](#) also found that reducing the speed of both sets of dots in a bidirectional RDK increased the size of the conventional direction illusion considerably. The inverse relationship reported here of stimulus speed to the size of the shift in perceived direction is thus consistent with the proposal that the statically-induced direction illusion and the conventional direction illusion share a common mechanism.

#### 5. General discussion

[Dakin and Mareschal \(2000\)](#) argued that mutual inhibition between direction-selective channels does not explain certain aspects of the direction illusion and proposed instead that the phenomenon arises as a result of the differential processing of object-relative and non-object-relative motion components. Without evidence solid enough to refute the distribution-shift model (see Section 1.2), however, subsequent studies have continued to attribute the direction illusion to mutual inhibition between direction-selective channels (e.g. [Braddick, Wishart, & Curran, 2002](#); [Chen, Matthews, & Qian, 2001](#); [Curran, Clifford, & Benton, 2006, 2009](#)). The primary aim of the current paper was to evaluate and compare the tenability of the distribution-shift and differential processing models of direction perception, particularly as they apply to the direction illusion. In Experiment 1, we observed a statically-induced direction illusion, an effect predicted by the differential processing model but not by the distribution-shift model. In Experiment 2, we found that

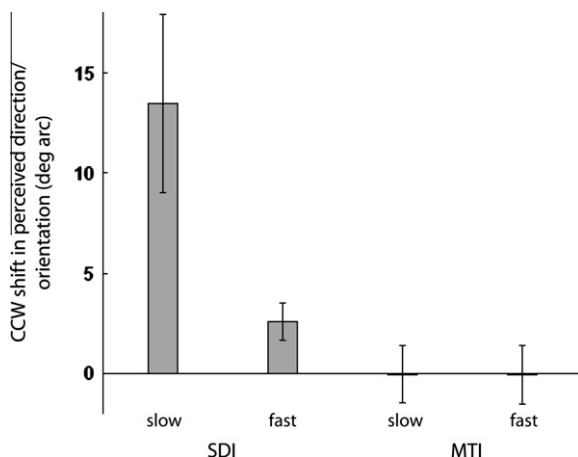


Fig. 7. Graph showing the results of Experiment 3. Error bars represent 95% confidence intervals.



introducing a static line parallel to the object-relative component direction of a direction illusion-invoking bidirectional RDK eliminated the illusion, while a line parallel to the non-object-relative component had no effect on the illusion. Again, the results are consistent with differential processing but not with mutual inhibition between direction-selective channels. In Experiment 3, we investigated the possibility that the results of Experiments 1 and 2 may be accounted for by the distribution-shift model applied to the orientation domain, hypothesising that the statically-induced direction illusion might arise from mutual inhibition between orientation-selective channels due to the existence of motion streaks. We measured the illusion with slow and fast moving dots and found the former to produce a larger effect. We also tested for the occurrence of a motion-induced tilt illusion due to slow and fast dot motion but found no effect. The results conflicted with the orientation distribution-shift hypothesis but were consistent with the differential processing model.

### 5.1. A third model – the clustering algorithm

One group of researchers (Mahani, Carlsson, & Wessel, 2005) has argued against the distribution-shift model, suggesting instead that the direction illusion occurs as a direct consequence of solving the motion transparency problem. They claim that implementation of a particular clustering algorithm, an iterative statistical process that is required to estimate the direction and group identity of the individual dots, necessarily leads to an exaggeration of the directional difference between the two dot sets. In other words, the direction illusion is a statistically inevitable by-product of the process of integration and segmentation of the independent elements in transparent motion. The results of Experiments 1 and 3, however, clearly demonstrate that directional shifts occur without any need for group identification since there was only one group present. In addition, the direction illusion was eliminated in Experiment 2 by the orientation of a static line, a result on which the clustering algorithm is silent. As such, the current results cannot be accounted for by the model of Mahani, Carlsson, and Wessel (2005).

### 5.2. Conclusion

We have shown that a static line can invoke shifts in the perceived direction of a moving stimulus and can eliminate the directional shift observed in a conventional direction illusion-inducing configuration. We have further shown that the direction shifts invoked by the static line cannot be explained by the existence of motion streaks. These findings cannot be attributed to a distribution shift resulting from mutual inhibition between either direction-selective or orientation-selective channels, and they pose serious questions about the distribution-shift model's adequacy in accounting for perceived direction in general. Conversely, the results reported here are consistent with the occurrence of differential processing of object-relative and non-object-relative component velocities by the visual system. Since moving objects usually have veridical velocities that comprise both types of motion, and since the latter type has been found to be underestimated with respect to the former, the differential processing model dictates that the perceived direction of such objects will be shifted from the veridical. We will be assessing the tenability of this model further in a future study on the effects of such processes on perceived stimulus velocity, i.e. direction and speed.

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